SUBMERSION OF *DUGALDIA* AND *PLUMMERA* IN *HYMENOXYS* (ASTERACEAE: HELIANTHEAE: GAILLARDIINAE)

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ABSTRACT

Dugaldia Cass. and *Plummera* A. Gray are herein recognized as subgenera of *Hymenoxys* Cass. Morphologic, cytologic, and chemical data are all consistent with this treatment. The appropriate new combinations and a new name are presented.

RESUMEN

Se reconocen *Dugaldia* Cass. y *Plummera* A. Gray como subgeneros de *Hymenoxys* Cass. Los datos morfolóicos, citológicos y químicos son consistentes con este tratamiento. Se presentan combinacions nuevas y un nombre nuevo.

INTRODUCTION

Generic level taxonomy in subtribe Gaillardiinae has long been problematic. Depending on which taxa are included in or excluded from the subtribe and how the included taxa are delimited into genera, subtribe Gaillardiinae might contain as few as two genera (*Gaillardia* Foug. and *Helenium* L.) or more than 25 genera.

With regard to *Dugaldia* Cass. and *Plummera* A. Gray, questions have arisen as to whether they should continue to be recognized as genera or submerged within *Hymenoxys* Cass. When I resurrected *Dugaldia* (Bierner 1974), those taxa were being treated as congeneric with *Helenium* by most workers (e.g., Gray 1874; Standley 1940). It has been clear for some time, however, not only that they are morphologically and chemically very different from taxa in *Helenium*, but that they are morphologically and chemically very similar to taxa in *Hymenoxys* (e.g., Bierner 1978). Likewise, the taxa included in *Plummera* have been recognized for quite some time as being very similar to taxa in *Hymenoxys* (Bierner 1978), and it had even been suggested earlier (Turner et al. 1973) that *Plummera* be combined with *Hymenoxys*.

Consideration of these questions in light of recent micromolecular chemical studies (Spring et al. 1994) and chloroplast DNA restriction site analyses (Bierner and Jansen unpublished) has led me to the conclusion that indeed *Dugaldia* and *Plummera* should be combined with *Hymenoxys* and

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recognized as subgenera. For purposes of this discussion, *Hymenoxys* is considered to include taxa that at times have been segregated into the genera *Macdougalia* A. Heller, *Phileozera* Buckley, *Picradenia* Hook., and *Rydbergia* Greene, but not taxa that can be segregated as *Tetraneuris* Greene (see Table 1).

DISCUSSION

Morphology

The taxa of *Dugaldia* are similar morphologically to *Hymenoxys brandegei* (Porter ex A. Gray) K.L. Parker, *H. grandiflora* (Torr. & A. Gray) K.L. Parker, and *H. insignis* (A. Gray ex S. Watson) Cockerell, which are members of *Hymenoxys* subgenus *Rydbergia* (Table 1). In particular, the involucral bracts of these taxa are organized into two to four subequal series, and the outer bracts are usually densely lanate toward their bases. The leaves of the *Dugaldia* taxa tend to be entire, while those of the *Hymenoxys* taxa tend to be divided; however, *Dugaldia integrifolia* (Kunth) Cass. often has upper and middle leaves that are deeply three-toothed, and *Hymenoxys brandegei* sometimes has all of its leaves entire.

The *Plummera* taxa are very similar morphologically to taxa in several of the *Hymenoxys* subgenera (Table 1). These similarities include involucral bracts that are in two unequal series with the outer bracts united, and leaves that are divided into linear segments. The disc florets of *Hymenoxys* and *Dugaldia*, however, are hermaphroditic, while those of *Plummera* are functionally staminate.

Cytology

Except for reports of dysploidy in *Hymenoxys odorata* DC. (e.g., Sanderson and Strother 1973) and *H. texana* (J.M. Coult. & Rose) Cockerell (Strother and Brown 1988) of subgenus *Phileozera*, the taxa of *Hymenoxys*, *Dugaldia*, and *Plummera* consistently have the same chromosome number, $n = 15$ (e.g., Beaman and Turner 1962; Bierner 1974; Sanderson 1973; Speese and Baldwin 1952; Strother 1966; Turner et al. 1973; Table 1). No polyploidy has been reported in any of these taxa, but polyploidy has been reported in some taxa of *Tetraneuris* (Johnston and Bonde 1969; Parker 1970; Speese and Baldwin 1952; Strother 1966, 1972).

Flavonoid, Monoterpene, and Sesquiterpene Lactone Chemistry

Hymenoxys, *Dugaldia*, and *Plummera* are extremely similar chemically (Table 1). All of them produce similar or identical 6-methoxy flavone aglycones, flavonol aglycones, flavonol glycosides, and 3-*O*-acetyl flavonol glycosides (Bierner 1974, 1978, 1994, unpublished; Sanderson 1975; Wagner et al. 1971, 1972a, 1972b). Taxa of *Tetraneuris*, however, have been found to produce 6, 8-dimethoxy flavone aglycones rather than 6-methoxy

TABLE 1. Comparison of *Dugaldia* and *Plummera* with *Hymenoxys* and *Tetraneuris*.

TAXON	MORPHOLOGY	CYTOLOGY	FLAVONOIDS AND MONOTERPENES	SESQUITERPENE LACTONES
Hymenoxys subg. *Hymenoxys*	Annuals Bracts in 2 unequal series Outer bracts united Outer bracts not lanate Plants caulescent Leaves dissected Disc flowers hermaphroditic	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides
Hymenoxys subg. *Phileozera**	Annuals Bracts in 2 unequal series Outer bracts united Outer bracts not lanate Plants caulescent Leaves dissected or entire to toothed (*H. texana*) Disc flowers hermaphroditic	$n = 3, 8, 11, 12, 14, 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides Monoterpene glycosides present only in *H. texana*	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides present or absent (*H. texana*)
Hymenoxys subg. *Picradenia*	Biennials and perennials Bracts in 2 unequal series Outer bracts united Outer bracts not lanate Plants caulescent Leaves dissected Disc flowers hermaphroditic	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides
Hymenoxys subg. *Macdougalia*	Perennial Bracts in 2 unequal series Outer bracts free Outer bracts lanate Plants caulescent Leaves entire Disc flowers hermaphroditic	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides

TABLE 1. Comparison of *Dugaldia* and *Plummera* with *Hymenoxys* and *Tetraneuris*. *(continued)*

TAXON	MORPHOLOGY	CYTOLOGY	FLAVONOIDS AND MONOTERPENES	SESQUITERPENE LACTONES
Hymenoxys subg. *Rydbergia*	Perennials Bracts in 3 subequal series Outer bracts free Outer bracts lanate Plants caulescent Leaves usually dissected Disc flowers hermaphroditic	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides
Dugaldia	Perennials Bracts in 2 to 4 subequal series Outer bracts free or united Outer bracts lanate Plants caulescent Leaves usually entire Disc flowers hermaphroditic	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides
Plummera	Perennials Bracts in 2 unequal series Outer bracts united Outer bracts not lanate Plants caulescent Leaves dissected Disc flowers staminate	$n = 15$	6-Methoxy flavone aglycones Flavonol aglycones Flavonol glycosides Flavonol 3-*O*-acetyl glycosides	Guaianolides Pseudoguaianolides Seco-pseudoguaianolides
Tetraneuris	Annuals and perennials Bracts in 2 subequal series Outer bracts free Outer bracts not lanate Plants caulescent or acaulescent Leaves usually entire Disc flowers hermaphroditic	$n = 14, 15, 28, 30, 45$	6, 8-dimethoxy flavone aglycones Flavonol aglycones Flavonol glycosides Monoterpene glycosides	Guaianolides Pseudoguaianolides

**Hymenoxys texana* is tentatively placed in subgenus *Phileozera* with *H. odorata* and *H. chrysanthemoides*, mainly on the basis of its annual habit. However, it is anomalous in this group with regard to its leaves (entire to toothed), chromosome number ($n = 3$ and 8), and chemistry (monoterpene glycosides present and seco-pseudoguaianolides absent). It has not been examined for flavonoids.

flavone aglycones (Bierner unpublished; Thomas and Mabry 1967, 1968a, 1968b), and none has been found to produce 3-*O*-acetyl flavonol glycosides.

With the exception of *Hymenoxys texana* (tentatively placed in subgenus *Phileozera*), monoterpene glycosides have not be detected in *Hymenoxys*, *Dugaldia*, or *Plummera* (Spring et al. 1994). Monoterpene glycosides have been found, however, in all of the *Tetraneuris* taxa (Spring et al. 1994).

Hymenoxys (except for *H. texana)*, *Dugaldia*, and *Plummera* all produce similar or identical guaianolides, pseudoguaianolides, and seco-pseudoguaianolides (Bohlmann et al. 1985; Hill et al. 1977; Ivie et al. 1976; Romo de Vivar et al. 1987; Seaman 1982; Spring et al. 1994). *Tetraneuris* taxa again are somewhat different; they produce guaianolides and pseudoguaianolides, but seco-pseudoguaianolides have not yet been found (Seaman 1982; Spring et al. 1994).

Chloroplast DNA

Recently, I worked with Robert K. Jansen at the University of Texas at Austin on chloroplast DNA restriction site analyses of many of these taxa (this work is being prepared for separate publication). Subgenera *Hymenoxys* and *Rydbergia* were not represented, but one species of *Dugaldia* (*D. hoopesii* [A. Gray] Rydb.) and both species of *Plummera* were included. In the phylogenetic analysis of the data, the *Dugaldia* and *Plummera* taxa were very strongly supported as being in the same branch of the chloroplast DNA phylogenetic tree with the taxa of *Hymenoxys* subgenera *Macdougalia*, *Phileozera*, and *Picradenia*, while the taxa of *Tetraneuris* were separated with strong confidence into a separate branch.

TAXONOMY

Hymenoxys Cass., Dict. Sci. Nat. 55:278. 1828. TYPE SPECIES: *Hymenopappus anthemoides* Juss., Ann. Mus. Natl. Hist. Nat. [Paris] 2:426. 1803.

Hymenoxys subgenus **Dugaldia** (Cass.) Bierner, stat. nov. BASIONYM: Dugaldia Cass., Dict. Sci. Nat. 55:270. 1828. TYPE SPECIES: *Actinea integrifolia* Kunth.

Oxylepis Benth., Pl. Hartw. 87. 1841. TYPE SPECIES: *Oxylepis lanata* Benth.

Hymenoxys integrifolia (Kunth) Bierner, comb. nov. BASIONYM: *Actinea integrifolia* Kunth, Nov. Gen. et Sp. 4:297. t. 410. 1820. *Dugaldia integrifolia* (Kunth) Cass., Dict. Sci. Nat. 55:270. 1828. *Cephalophora integrifolia* (Kunth) Steud., Nom. ed. 2. 1(3):328. 1840. *Helenium integrifolia* [sic] (Kunth) Benth. & Hook. ex Hemsl., Biol. Centr. Amer. Bot. 2:227. 1881. *Heleniastrum integrifolium* (Kunth) Kuntze, Revis. Gen. Pl. 1:342. 1891. TYPE: MÉXICO. HIDALGO: "...inter Omitlán et Serro del Jacal, alt. 1400 hex." *Humboldt & Bonpland s.n.* (HOLOTYPE: P!).

Oxylepis lanata Benth., Pl. Hartw. 87. 1841. *Helenium lanatum* (Benth.) A. Gray, Proc. Amer. Acad. Arts 9:205. 1874. TYPE: GUATEMALA: "In summo monte Cumbre de Argueta dicto," *Hartweg 593* (HOLOTYPE: K!; ISOTYPE: P!).

Hymenoxys hoopesii (A. Gray) Bierner, comb. nov. BASIONYM: *Helenium hoopesii* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863:65. 1864. *Heleniastrum hoopesii* (A. Gray) Kuntze, Revis. Gen. Pl. 1:342. 1891. *Dugaldia hoopesii* (A. Gray) Rydb., Mem. New York Bot. Gard. 1:425. 1900. TYPE: UNITED STATES. COLORADO: "South Park and west of Pike's Peak," *Hall & Harbour 272* (HOLOTYPE: GH!; ISOTYPES: MO!, NY!, PH!).

Hymenoxys pinetorum (Standl.) Bierner, comb. nov. BASIONYM: *Helenium pinetorum* Standl., Field Mus. Pub. Bot. 22:127. 1940. *Dugaldia pinetorum* (Standl.) Bierner, Brittonia 26:391. 1974. TYPE: MÉXICO. NUEVO LEÓN: "Sierra Madre Oriental, ascent of Sierra Potosí by north hogback, about 20 mi NE of Galeana, abundant in upper pine forest, alt. 3390 meters." 26 Jul 1934, *C.H. & M.T. Mueller 1258* (HOLOTYPE: F!).

The species of *Hymenoxys* subgenus *Dugaldia* are well defined and have already been treated taxonomically (Bierner 1974).

Hymenoxys subgenus **Plummera** (A. Gray) Bierner, stat. nov. BASIONYM: *Plummera* A. Gray, Proc. Amer. Acad. Arts 17:215. 1882. TYPE SPECIES: *Plummera floribunda* A. Gray.

Hymenoxys microcephala Bierner, nom. nov. BASIONYM: *Plummera floribunda* A. Gray, Proc. Amer. Acad. Arts 17:215. 1882. non *Hymenoxys floribunda* (A. Gray) Cockerell, Bull. Torrey Bot. Club 31:485. 1904. TYPE: UNITED STATES. ARIZONA: Cochise Co.: "Apache Pass, Chirricahua [sic] Mountains," Sep 1881, *Lemmon & Lemmon 352* (HOLOTYPE: GH!; ISOTYPES: BM!, F-207616!, GH!, K [photo at F-1645644!], NDG-061757!, PH-two sheets!, US-47542!; PROBABLE ISOTYPES: F-313722!, MO-3726424!, NDG-061758!, NY!).

Hymenoxys ambigens (S.F. Blake) Bierner, comb. nov. BASIONYM: *Plummera ambigens* S.F. Blake, J. Wash. Acad. Sci. 19:276. 1929. TYPE: UNITED STATES. ARIZONA: Graham Co.: "Fairly common on lower slopes of Mt. Graham, ca. 1370 m, 22 Jul 1927, *Peebles, Harrison & Kearney 4395* (HOLOTYPE: US-1436073!, photo at NMC!; ISOTYPE: GH!).

The two taxa of *Hymenoxys* subgenus *Plummera* could be treated as varieties of a single species, as suggested by Turner et al. (1973). I agree that morphologic differences between the two are slight, but the taxa appear to be geographically isolated from one another without a zone of contact and intergradation. Furthermore, Spring et al. (1994) found several differences between them with regard to sesquiterpene lactone substituents and side chains. For now, the conservative approach of continuing to recognize them as distinct species seems more appropriate.

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